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13. ABSTRACT (Maximum 200 words) <p>Field studies indicate that the distribution of benthic invertebrate larvae in the plankton around Fieberling Guyot is strongly influenced by topographically-modified mesoscale flows. An anticyclonic circulation feature was observed over the seamount, with flows oriented outward near the surface of the seamount, and inward several hundred meters above. Larval distributions were compressed vertically near the seamount, but extended laterally 10's of km at the level of the seamount summit - a result that is consistent with the downwelling and outwelling flows observed near the seamount summit. These results indicate that larvae are not retained directly above the seamount in a Taylor Cap, but may be retained in the larger-scale circulation feature.</p> <p>During the course of the project, a new recruitment panel for quantitative larval studies was designed, seasonal spawning of several seamount coral species was observed, and enhanced abundances of seabirds were documented near the seamount. On Volcano 7, a striking benthic zonation pattern corresponded to the vertical excursion of the oxygen minimum as it cycled diurnally in internal waves - in effect producing a deep-sea intertidal zone.</p>				
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DISPERSAL AND RETENTION OF BENTHIC INVERTEBRATE LARVAE IN FLOWS NEAR A SEAMOUNT

A Final Report on Grant N00014-89-J-1431
From the Office of Naval Research (Oceanic Biology Program)
For the Period of Jan. 1, 1989 - Dec. 31, 1993
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INTRODUCTION

The retention of larvae by flow processes is, for many benthic species, a critical mechanism for successful recruitment back into a habitat, and often ensures persistence of the local population. This phenomenon has been demonstrated for a variety of estuarine invertebrate species, and more recently for coral reef inhabitants. I suggest that retention of water masses and larvae may also occur on oceanic seamounts, allowing larvae to recolonize their source habitats, rather than being advected away with little chance of reaching another suitable seamount. Ocean currents and tides have been shown to interact with seamount topography to produce mesoscale circulation above, and in the wake of, a seamount. The objective of my research group's study has been to determine whether seamount-modified flows influence the dispersal of larval invertebrates, and retain them for sufficiently long to enhance their recruitment into source populations. Our long-term goal is to quantify the effect of flow-mediated dispersal and retention on benthic population dynamics and on gene flow among seamounts.

APPROACH

We have been testing our hypothesis of flow-mediated larval retention in field studies of Fieberling Guyot, a tall isolated seamount in the eastern subtropical Pacific (32.5°N, 127.75°W). We generate expected larval distribution patterns near the seamount using a model of passive larval dispersal in mesoscale flows that is derived from empirical and theoretical studies of the physical oceanography near Fieberling. These predicted patterns are then compared to observed larval distributions, that have been quantified with plankton tows and recruitment panels, to determine the extent to which flow processes control larval patterns. We evaluate assumptions in our dispersal model (e.g., larvae as passive particles; dispersal from a well-mixed, continuous larval source in the benthic boundary layer) and alternative hypotheses (including the effects of discontinuous reproduction or larval behavior) by analyzing supplementary data on the reproductive modes, distributions and fecundities of the adults, and by sampling the plankton repeatedly over several years.

Preliminary observations from a pilot current meter mooring (deployed 1989-1990) and theoretical modeling by Dave Chapman and Dale Haidvogel suggested that a Taylor cap should occur consistently over Fieberling, enhancing water residence times within a cap-shaped region extending vertically several hundred meters above the seamount surface, and horizontally along the flank to a depth of roughly 1500 m. We predicted that the enhanced water residence times should retain larvae released from the seamount populations, resulting in higher larval abundances in the plankton within the flow feature (Mullineaux 1994, *Implications of mesoscale flows for dispersal and retention of larvae in deep-sea habitats*. In: Young & Eckelbarger, eds. *Reproduction, larval biology and recruitment of the deep-sea benthos*. Columbia University Press). Thus our sampling efforts were designed to quantify larval abundances within the bottom trapped flow feature and compare them with abundances further from the seamount.

We sampled larvae over a period of two years in the plankton near Fieberling Guyot

Fieberling Cruises

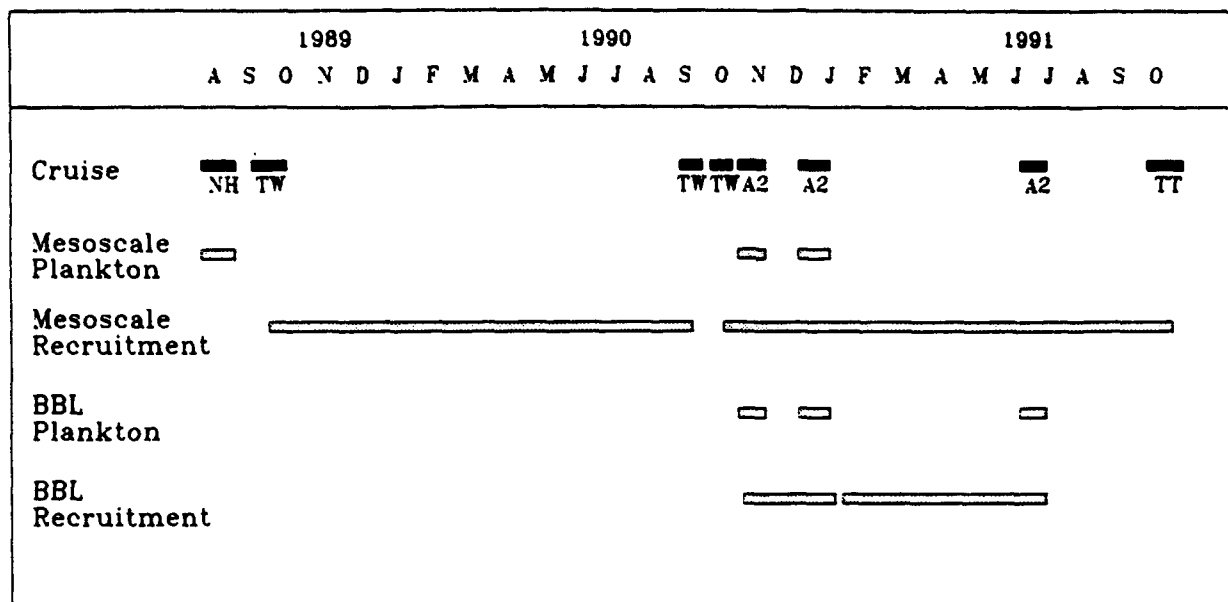


Fig. 1. Larval sampling schedule on Fieberling Guyot. Mesoscale plankton sampling was conducted on three cruises with a 1/4 m² MOCNESS system, using nine nets of 64 µm mesh. Plankton were sampled in the benthic boundary layer (BBL) with a smaller three-net system towed by the submersible ALVIN. Recruitment panels were attached to a pilot mooring in 1989-1990, and to moorings in a mesoscale array in 1990-1991. Recruitment panels were also deployed in the BBL for 3-mo and 6-mo durations. Ships identified as NH (New Horizon), TW (Thomas Washington), A2 (Atlantis II), and TT (Thomas Thompson).

using a 9-net 1/4m² MOCNESS, a 3-net system towed by ALVIN, and an array of recruitment panels (Fig. 1). Sampling was focussed at depths of 500 and 1500 m above the summit and flank of the seamount, and at comparable depths up to 40 km away over the abyssal seafloor (Fig. 2). Net samples provide a "snapshot" of larval distributions at a single point in time, and have the advantage of including all species larger than the net mesh size (64µm). Recruitment panels expand this approach by integrating over longer time scales and by including species that are too small or indistinct as larvae to be collected and analyzed from net tows. Recruitment plates have the disadvantage of excluding species with specific settlement cues or requirements, but they do reveal which larval species in the plankton have reached competency (ability to settle) on time scales of the retentive flow features.

RESULTS

New Recruitment Panel Design for Quantitative Larval Studies. Using flume and shallow field studies we have designed recruitment panels that are useful for quantitative studies of larval abundances in the plankton (*Garland & Mullineaux 1992, Particle contact on flat plates in flow: a model for initial larval contact, WHOI Tech. Rep. 92-26; Mullineaux & Garland 1993, Field experiments on larval settlement in manipulated boundary-layer flows, Mar. Biol. 116:667*). Two important features of our recruitment

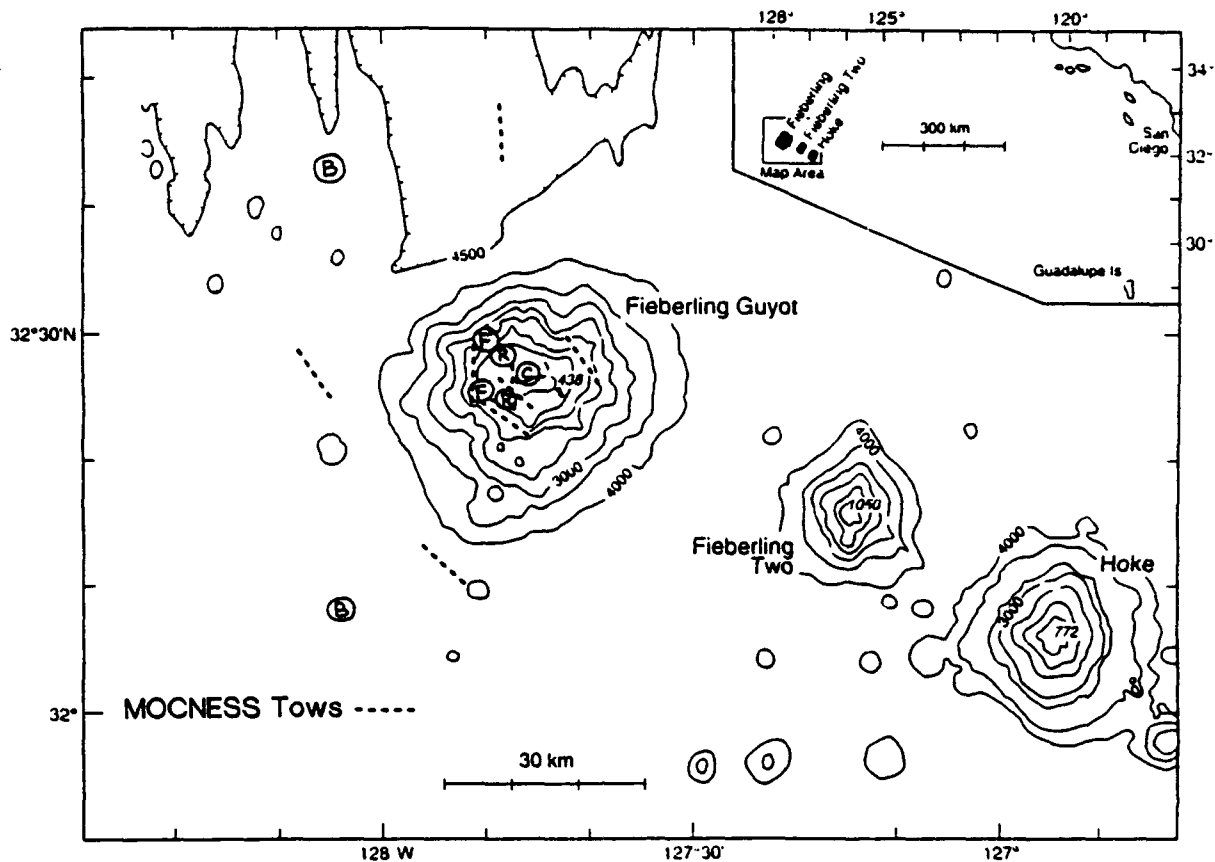


Fig. 2. Location of nine MOCNESS tows (Oct. 1990) and moored array of current meters and recruitment panels (deployed 1990-1991) on Fieberling Guyot. Three tows, consisting of eight sequential net samples, were positioned over each of three regions: the summit (500 m depth), flank (500 and 1500 m depth) and away from the seamount (500 and 1500 m depth). A similar MOCNESS sampling design was used in Sept. 1989 and Dec. 1990. Recruitment panels were supported on moorings at the center (C), rim (R), flank (F) and base (B), positioned in clusters near the bottom, at 500 m depth, and (on the deeper moorings) at 1500 m depth. Additional moorings (not shown) were deployed for shorter intervals (3-mo and 6-mo) near the C mooring and the northwest R mooring to investigate larval patterns in the boundary layer.

studies are: (1) we can determine which regions of the plates are suitable for assessing larval concentrations, and avoid those which are strongly influenced by small-scale flow effects; and (2) we can calculate relative differences in larval abundance in the water column from differences in recruitment on the plates, even over a wide range of flow velocities. These features have allowed us to interpret patterns of larval recruitment on panel arrays over Fieberling Guyot in terms of relative differences in larval abundance.

No Taylor Cap Exists at Fieberling. Although the preliminary results of flow and larval studies during the 1989-1990 season showed anticyclonic circulation and elevated larval abundances at Fieberling's summit (consistent with a scenario of larval retention by a Taylor cap), the in-depth study of 1990-1991 revealed a quite different pattern. Analyses by Ken Brink, Dale Haidvogel, and others showed that the anticyclonic circulation, instead of being indicative of a Taylor cap with upwelling at the seamount center, was part of a flow feature with downwelling at the center and outwelling near the bottom. In addition,

measurements by John Toole, Eric Kunze and Ray Schmitt showed that turbulence near the seamount was unusually high for open-ocean waters at this depth, suggesting that water residence times were not elevated directly above the seamount. Because no bottom-trapped retention was occurring, we no longer expected larval abundances to be elevated near the seamount summit and flank. Indeed, total larval abundances near the seamount surface, measured in both the plankton tows and the recruitment panels from the 1990-1991 season, were only slightly higher than abundances at the same depth up to 40 km away. This slight elevation in abundance can be explained by a steady-state diffusion model and is not likely due to bottom-trapped retention (*Mullineaux (in prep). Influence of mesoscale flows on dispersal and retention of benthic larvae near a tall seamount*). Larval abundances, however, were high relative to those reported previously from deep, open-ocean samples, making us wonder if abundances decreased at distances greater than 40 km. In addition, larvae of a few taxa were found only near the seamount, despite the high turbulence levels that should have mixed them quickly away. These two observations are put in context below.

Mesoscale Flows Induce Unique Larval Dispersal Patterns. Although mesoscale flows near Fieberling Guyot do not appear to retain larvae in a bottom-trapped Taylor cap, these flows clearly influence larval dispersal of the seamount benthos. Striking patterns in the vertical distributions of larvae were apparent in recruitment arrays near the seafloor, with most larval individuals occurring within a few tens of meters of the seamount surface. This latter observation of compressed vertical distributions is surprising given the elevated turbulence levels near the seamount surface. We believe the most likely explanation for the compressed vertical, and extensive horizontal, larval distributions is that dispersal in the vertical direction is impeded by the central downwelling flows, and dispersal in the horizontal is facilitated by advection off the seamount in the outward, near-bottom flows (*Mullineaux, Kunze, Gross & Mills (in prep). Larval transport and boundary-layer mixing from benthic communities on Fieberling Guyot*). Before we discard completely the idea of larval retention near seamounts, however, it is important to note that the flows described over Fieberling are part of a large-scale circulation cell with upwelling at the edges and inwelling at the top. Such a flow could potentially retain larvae released from the seamount (possibly resulting in elevated abundances even 10's of km away from the seamount), but larval accumulation and elevated abundances would occur on scales larger than those we sampled. Clearly, a more widely-spaced sampling array is needed to evaluate the potential for larval retention on the larger scale.

Species-Specific Dispersal Patterns - Are Some Larvae Not Passive? Several of the taxa sampled over Fieberling in the plankton tows and recruitment panels are significantly more abundant over the seamount summit and a few (in particular, a barnacle and a serpulid worm) are found exclusively at the summit. Do these species have special life-history or behavioral adaptations that prevent them from being mixed away from their source habitat? We are evaluating this possibility, as well as alternatives (such as fortuitous sampling of a reproductive pulse-event) for a variety of taxa, using time-series samples of larval abundance in the plankton, and of adult reproductive status (*Mullineaux, Mills & Williams (in prep.). Reproductive and larval ecology of benthic invertebrates on a deep seamount*).

Related Projects: Deep-Sea Intertidal, Population Genetics and Seabirds. I have been involved with several related seamount projects that were partially supported under this grant. During an expedition to Volcano 7 (a seamount off the coast of Mexico), a research team led by Karen Wishner investigated the interaction of water-column processes in the oxygen minimum with benthic processes on the slopes of the seamount that intersected it. In particular, we found striking benthic zonation on the seamount that corresponded to the vertical excursion of the oxygen minimum as it cycled diurnally in internal waves - in effect, producing a deep-sea intertidal zone (*Wishner, Levin, Gowing & Mullineaux 1990, Involvement of the oxygen minimum in benthic zonation of a deep seamount. Nature 346: 57-59; Wishner, Ashjian, Gelfman, Gowing, Kann, Levin, Mullineaux & Saltzman (in press). The lower interface of the eastern tropical pacific oxygen minimum zone. Deep-Sea Res.*).

During one of my cruises to Fieberling, a WHOI Postdoc, Chris Haney, was able to document elevated seabird abundance over the seamount (*Haney, Haury, Fey & Mullineaux (in revision), Seabird aggregation at a deep North Pacific seamount, Mar. Ecol. Prog. Ser.*). Although anecdotes of seabird aggregations over seamounts occur in the literature, the observations are rarely quantified or substantiated, making Haney et al.'s contribution one of the first quantitative demonstrations of this phenomenon.

Our benthic studies on dispersal at Fieberling Guyot have now expanded to a study of population genetics of seamount corals on Fieberling and several other subtropical Pacific seamounts. We are hypothesizing that dispersal between geographically isolated seamounts is infrequent, except where currents reduce the dispersal time, such as along seamount chains where rectified flows are oriented parallel to the chain. Scott France (WHOI postdoc), Ewann Agenbrood (WHOI Joint Program student) and I are currently testing this hypothesis by sequencing DNA from several coral species and looking for genetic diversity within and between populations.

SIGNIFICANCE

The similarity between observed patterns of larval distribution near Fieberling Guyot and those predicted from topographically-induced mesoscale flows provides strong evidence that these flows play an important and predictable role in larval dispersal of seamount benthos. Thus, knowledge of mesoscale flows gives us a predictive capability in studies of larval transport and gene flow between deep-water benthic habitats. The absence of a bottom-trapped Taylor cap, and associated larval aggregation, does not preclude the possibility of larval retention in a larger-scale circulation feature, but our measurements were clustered too tightly around the seamount to allow for more than speculation about this possibility. Prior to this study, very little information existed on larval abundance and transport in open-ocean benthic habitats, and no benthic invertebrate larvae had been sampled near seamounts. Our plankton samples, collected repeatedly over a period of two years, provide a unique database of the spatial patterns and seasonality of larval dispersal in deep-water habitats. We expect that they will become a baseline for future efforts to understand dispersal, population dynamics and gene flow in the deep ocean.

Publications Supported by this Grant

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- Wishner, K.F., C.J. Ashjian, C. Gelfman, M.M. Gowing, L. Kann, L.A. Levin, L.S. Mullineaux and J. Saltzman. 1994. The lower interface of the eastern tropical pacific oxygen minimum zone. *Deep-Sea Res.* (in press).
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- Mullineaux, L.S. Influence of mesoscale flows on dispersal and retention of benthic larvae near a tall seamount. (for *Journal of Marine Research*)
- Mullineaux, L.S., T.F. Gross, E. Kunze and S.W. Mills. Larval transport and boundary-layer mixing from benthic communities on Fieberling Guyot. (for *Deep-Sea Research*)
- Mullineaux, L.S., S.W. Mills and I.P. Williams. Reproductive and larval ecology of benthic invertebrates on a deep seamount. (for *Marine Biology*)

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- 1989 Mullineaux, L. S. Vertical transport of benthic invertebrate propagules in flows over Volcano 7 seamount. *Trans. Am. Geophys. Un.* 71:155.